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Mutual ornamentation, sexual selection, and social dominance in the black swan

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We investigated the adaptive significance of a sexually monomorphic ornament in the black swan *Cygnus atratus*. Both sexes grow curled feathers on their wings (range 7–22 curled feathers per wing), which are displayed prominently in a range of social interactions. The number of curled feathers increased until the birds reached sexual maturity (at 2 years of age) but did not vary with age thereafter. We found evidence for both sexual and social functions of the ornament. Paired, mature individuals of both sexes had higher numbers of curled feathers than unpaired, mature birds, and individuals paired assortatively with respect to curled feather number, suggesting the feathers may be involved in mutual sexual selection. More ornamented individuals were dominant in agonistic interactions with birds of the same sex and pairing status. Highly ornamented pairs were also more likely to maintain extended tenancy of preferred cygnet feeding areas, which resulted in improved offspring survival. The curled feathers thus appear to function as a signal of social dominance, which is highly correlated with reproductive success and is therefore a reliable signal of parental quality in mate choice. *Key words:* black swans, *Cygnus atratus*, dominance, mutual sexual selection, ornamentation, signaling, social selection. *[Behav Ecol 15:380–389 (2004)]*

Empirical studies of sexual selection during the past few decades have focused predominantly on organisms with sexually dimorphic traits, in which trait elaboration is typically restricted to males. There is now abundant evidence that male–male competition and female choice can lead to extravagant ornamentation among males (Andersson, 1994). Yet in many species, ornamental traits occur in both sexes and are elaborated to a similar degree in males and females. Darwin (1871) proposed that such mutual ornamentation was a genetically correlated consequence of intense sexual selection on males. Under this scenario, traits selected for in males are also expressed in females simply because they also carry the genes for these traits (Lande, 1980, 1987; Lande and Arnold, 1985). However, empirical evidence in support of a genetic correlation in a plumage trait is limited to one study (Roulin et al., 2001). Furthermore, recent phylogenetic work has demonstrated that evolutionary transitions between dimorphism and monomorphism have occurred frequently and in both directions (Wiens, 2001), suggesting that such changes are relatively unconstrained by genetic correlations.

An alternative explanation for similar ornamentation in males and females is that sexual selection acts on both sexes. This idea was first proposed by Huxley (1914), who coined the term "mutual sexual selection." Recent models have demonstrated that mutual mate choice resulting in mutual ornamentation is a theoretically plausible process (Johnstone, 1997; Johnstone et al., 1996; Kokko and Johnstone, 2002). Experimental studies of crested auklets *Aethia cristatella* have provided evidence for both mutual mate choice (Jones and Hunter, 1993) and competition over access to mates in both sexes (Jones and Hunter, 1999).

Although ornamentation is typically associated with the process of sexual selection, there are also numerous examples of ornamental signals for which a sexual role is unlikely (Zahavi, 1991). Examples from avian studies include bright coloration restricted to juveniles (which may induce parents to feed the young; Lyon et al., 1994), song and displays of passerines on winter territories far from the breeding grounds (Zahavi, 1972), and extravagant group displays that function in social circumstances unrelated to sex (Zahavi, 1990). Perhaps the best studied examples of avian signaling in which a sexual context is absent or indirect are the badges of status, plumage signals of dominance in social competition over resources such as food and shelter (Butcher and Rohwer, 1989; Savalli, 1995; Whitfield, 1987).

The same signals that are used in competition over access to mates may be used in competition over access to other resources, and there is therefore no need to assume that such signals will be selected by different selection processes (Zahavi, 1991). However, because sexual selection is defined in a strict sexual context (Andersson, 1994; Darwin, 1871), the evolution of signals, both sexual and nonsexual, may be better understood in a wider context, such as signal selection (Zahavi, 1991) or social selection (Crook, 1972; Tanaka, 1996; West-Eberhard, 1983, 1984, 1991). Signal selection and social selection refer to the same process and can be defined as "the selective force that arises when a signal influences the fitness of signallers or both the fitness of signallers and receivers" (Tanaka, 1996: 512).

West-Eberhard (1983) suggested that bright coloration in both sexes of many birds may be attributed to the fact that, in such species, both sexes perform aggressive displays. So far, the only avian ornament that has been shown to be involved in aggressive displays in both sexes is the crest of the crested auklet (Jones and Hunter, 1999), but the same has been suspected in monochromatic species of hummingbirds (Bleiweiss, 1992). For such aggressive behavior to be adaptive, it must have a positive effect on survival or reproductive success in both sexes. This has not been demonstrated for any mutually ornamented species.

In this study we considered both potential sexual and nonsexual functions for a feather ornament found in both sexes of the black swan *Cygnus atratus*. Males and females

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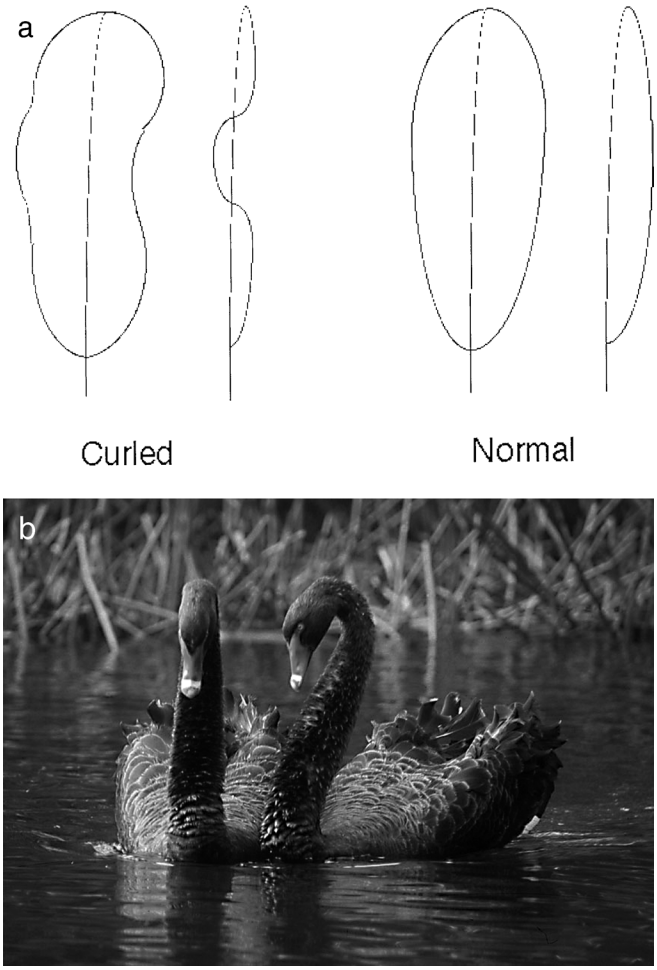

Figure 1
(a) A schematic representation of a curled feather (left) and a straight feather (right) viewed from above and from the side. (b) Black swans during agonistic interaction. Note the curled feathers on the wings, which become more prominent when the bird raises its wings during threat display.

have curled ornamental feathers on their wings, which are prominently displayed during agonistic encounters between individuals and as part of the triumph ceremony (Kraaijeveld and Mulder, 2002). These curled feathers have no obvious advantage in terms of natural selection and thus qualify as ornaments (Amundsen, 2000). Our aims were to (1) document variation in the number of curled feathers among and within individuals in relation to sex, age, body size, and condition, (2) test for a relation between ornamentation and social pair formation, and (3) assess whether the number of curled feathers is related to social dominance, access to feeding sites, and reproductive success. To our knowledge, this is the first study to investigate the relation between ornamentation and reproductive success in a species with an ornament that is expressed equally in males and females.

METHODS

Study species

Black swans are large (4–7 kg), long-lived, and socially monogamous waterfowl that occupy shallow wetlands, often at high densities (Frith, 1982). Both sexes have black plumage with conspicuous black curled tertials and wing coverts. Both sexes participate in incubation (Brugger and Taborsky, 1994) and brood defense. Black swans have a low divorce rate (6%; Kraaijeveld, unpublished data) and once formed, pairs tend to remain together. In captivity, black swans may breed successfully from 2 years of age (Braithwaite, 1981). The proportion of adults breeding in any year is highly variable, and only one successful nest is produced per pair per season.

Capture and measurement of birds

This study was conducted between 1999 and 2001 at Lake Wendouree, Ballarat, Australia (37°33′S, 143°49′E), a permanent lake of 238 ha supporting a population of about 170 black swans year-round. We lured the swans from the water with bread morsels and captured them by hand. Adults were caught during the breeding seasons (July–November) of 1999–2001 and during the prebreeding seasons (May–June) of 2000 and 2001. We fitted adults with metal bands (Australian Bird and Bat Banding Scheme) and individually colored and numbered plastic leg bands. The plastic bands could be read with binoculars from a distance of up to 30 m (when the bird was on land or up-ending to feed on submerged aquatic plants) or when the bird was in clear water within 5 m of the shore. We censused all banded individuals twice weekly during the breeding season (July–November) and monthly during the remainder of the year by walking around the perimeter of the lake (6 km) and marking the location of banded individuals on a map.

For each captured adult, we measured tarsus length (with callipers to the nearest 1 mm), bill and total head length (callipers; nearest 0.1 mm), wing length (butt-ended ruler; nearest 1 cm) body mass (spring balance; nearest 100 g), and the number of curled feathers on each wing (described below).

Although most adults can be sexed on behavior, size, and cloacal inspection, we confirmed the sex of all individuals using a molecular technique (Griffith et al., 1998). Captured birds were assigned to one of three age classes. First-year black swans are easily recognized by their gray plumage, dull bill color, and black tips of their primaries (Marchant and Higgins, 1990). Most second-year individuals retain black tips in some of their primaries (10–16 known 2-year-old birds had black tips of some primaries, compared to 0 of 30 adults known to be $\geq$3 years old). Individuals in black plumage with pure white primaries were at least 2 years or older and were classed as adults.

During the breeding season, we searched all available breeding habitat in a canoe once per week and plotted the location of nests on a map. We recorded the identity of the attending adults at each nest and the clutch size. Cygnets stayed in the nest for about 24 h after hatching and were then taken to the shore by their parents. Some cygnets were caught on the nest, but most were caught on shore, generally within the first week after hatching. We rounded up a brood together with their parents and caught all the cygnets simultaneously. At least one parent was also caught and retained while the cygnets were processed to ensure that cygnets were not separated from their parents. Cygnets were too small to be banded when first caught, so they were marked with a unique combination of small holes in the webs between their toes with a standard leather punch (see Braithwaite, 1981). These holes closed up as the cygnets grew to adult size, and there was no indication that this procedure had any harmful effect on the cygnets' health. The scars left by these punches were used for subsequent individual identification. We recaptured cygnets surviving to 8 months and subjected them to the same procedures as adults. Cygnets that had disappeared before this point were assumed to have died. This assumption is supported by a study of black swans in New Zealand in which

95–100% of ringed black swans recovered during their first year of life ($n = 1792$) were recovered on their natal lake (Williams, 1977).

All procedures used during this study were approved by the Animal Experimentation Ethics Committee of the University of Melbourne.

Ornamentation

We scored the degree of ornamentation for captured birds by counting the number of curled wing-feathers (tertials and wing coverts). A feather was defined as curled when part of at least one of the vanes reached above the central feather-shaft (rachis) when viewed from the side (Figure 1a). To determine whether this method was repeatable, we compared the feather counts of 22 individuals (13 males and 9 females) captured both in May and June 2000. The intraclass correlation coefficient (r_I; Zar, 1999) was positive and significantly different from zero ($n = 22$, $r_I = .89$, $F = 16.88$, $p < .001$), indicating that variation within individuals was significantly smaller than variation between individuals. The r_I value is high compared to those reported in similar studies of feather ornaments (e.g., 0.41, 0.45, 0.52, 0.58, and 0.74 for different ornaments of least auklet *Aethia pusilla*; Jones and Montgomerie, 1991).

We assessed possible changes in feather number with age in two ways. We first calculated mean feather counts for different age classes using individuals of known age (banded as nestlings or aged using the criteria listed above). Each individual contributed to this analysis only once. For individuals that were measured twice, we used the most recent measurement to maximize the sample size for older age classes. We were most interested in older age classes because first-year birds were excluded from all further analyses *a priori*. Some 2-year-old individuals with all-white primaries may have been falsely classified as adults. To examine whether this was likely to bias our results, we inspected known second-year birds for a correlation between the number of primaries with black spots and the number of curled feathers. We then compared repeated measurements from the same individuals across years.

We examined whether ornamentation was correlated with the body size or body condition of the individual. Tarsus length remains fixed when a bird reaches adult size and is considered the best univariate measure of body size (Rising and Somers, 1989). Therefore, the residuals from the regression of body mass on tarsus length were used as an index for body condition (Packard and Boardman, 1987).

Pairing status

If curled feathers are used in mate choice, we would expect to find systematic differences in ornamentation between paired and unpaired individuals, and possibly a correlation between the degree of ornamentation of members of a social pair. We identified pairs from census data. The male and female of a social pair maintain close proximity throughout the year, and social pairs were thus easily recognizable. Individuals were classed as paired if they attempted to breed together or if they were seen together on consecutive census dates over at least 3 months. This eliminates the possibility of mistaking trial liaisons (Choudhury and Black, 1993) between unpaired birds for long-term pairing because such associations never lasted for more than 3 weeks.

Social interactions

Black swans raise their wings and display the curled feathers in a range of social contexts, but especially during agonistic interactions. We identified the individuals involved and quantified the outcomes of spontaneous agonistic interactions as well as those induced by feeding during the prebreeding seasons (April–July) of 2000 and 2001. Agonistic interactions included threat displays (during which competing individuals raised their wings; Figure 1b), chases, and pecks. We included only interactions with an unambiguous winner in the analysis. An individual was considered to have won the interaction if its opponent flew off or walked away with lowered wings. The observations were conducted blind to the sex, pairing status, and number of curled feathers for each individual, which were determined retrospectively from capture records. To avoid pseudoreplication, we included each dyad into the analysis only once. In all cases for which multiple interactions between the same dyad were observed ($n = 32$), the same bird was the winner in all interactions.

In addition to opportunistic quantification of agonistic encounters, we conducted focal observations on pairs during the nonbreeding season (May–July 2000) and when they were accompanied by dependent cygnets during the breeding season (July–November 1999 and 2000). Each observation lasted 1 h, and each pair was observed once. We recorded the number of agonistic interactions in which one or both of the participants raised their wings; whether the male, female, or both individuals were involved in the interaction; and the duration for which individuals kept their wings raised. Individuals often raised their wings in anticipation of an interaction, so we report the total amount of time spent in threat display posture during the observation, rather than per interaction.

Residency and cygnet foraging

After hatching, parents led the precocial cygnets to feeding grounds on lawns surrounding the lake or shallow water close to the shore. Frequent agonistic interactions occurred between families over access to these feeding sites. We assessed the success of pairs in competing over these feeding areas by comparing the duration of their tenancy of these areas. Certain pairs were consistently seen at the same locations, while others were seen in different locations each time. We assumed that pairs with prolonged tenancy of particular patches were behaviorally dominant to those that continually moved between sites, and we classified pairs according to their tenure. Pairs that were found along the same 500-m stretch of foreshore for 3 or more subsequent weeks during the cygnet-raising period were classed as resident. The remaining pairs were classed as itinerant.

We examined whether residency was related to ornamentation and reproductive success. We also estimated the interruption cost of agonistic encounters between families on the cygnets' opportunity to feed by conducting focal observations on dependent cygnets. Each observation lasted 1.5 h, during which we recorded the proportion of time the cygnet spent feeding. In families with more than one cygnet, we recorded the time during which at least one of the cygnets was feeding, as the others would also have had the opportunity to feed during this time.

Statistical analyses

We only compared measurements of different parameters if they had been obtained in the same season. Morphological measurements other than count data that did not deviate from normality were analyzed using parametric tests. We analyzed count data (curled feathers, clutch size and brood size) using nonparametric tests. The distributions of frequency and length of agonistic interactions deviated from normality and

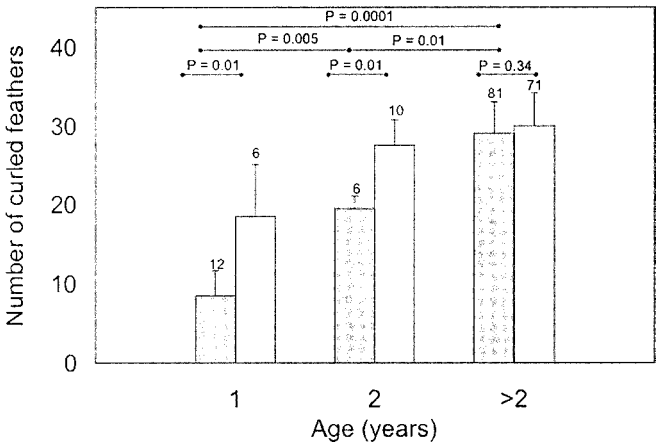

Figure 2
Median number of curled feathers among known age classes, with quartile deviation. Females: shaded bars, males: open bars. Each individual contributed to only one category in order to maximize the sample size for second-years. The results of post-hoc tests for differences between age classes in females are shown. Males did not differ between age classes. Differences between males and females within each age class were tested using Mann-Whitney *U* tests.

were also analyzed using nonparametric tests. Because residency status is an attribute of a pair, we used mid-pair values (calculated by averaging the male and female measurements) for analysis of traits in relation to residency. We analyzed residency status using binary logistic regression to test whether the effects of brood size and ornamentation were independent of each other. The test statistic in these analyses is the ratio of the coefficient over its standard error (*t* ratio; Systat, 1997). Cygnet survival to independence was analyzed using a generalized linear model with binomial error distribution and a logit link function. This analysis used the number of surviving cygnets per brood as the dependent variable and initial brood size as the binomial denominator. We assessed the significance of the independent variables from the change in deviance when the variable was removed from the model, which approximates a chi-square distribution (Beath, 2001). We used SYSTAT 7 (Systat, 1997) for all analyses, except generalized linear models, which were performed in GLMStat (Beath, 2001). Means are presented ± standard deviations. For non-normally distributed data, we present the median and the quartile deviation (Zar, 1999).

RESULTS

Curled feathers in relation to age and sex

The mean numbers of curled feathers for known-age (including those aged using the criteria described in the Methods) individuals of both sexes are illustrated in Figure 2. There was no significant correlation between the number of curled feathers and the number of primaries with black spots for either sex (males, $r_s = -.28$, $n = 10$, $p = .56$; females, $r_s = -.20$, $n = 6$, $p = .90$), and there is therefore no reason to assume that any second-year individuals with all-white primaries had unusually small or large numbers of curled feathers. The number of curled feathers differed significantly between females of different age classes (Kruskall-Wallis $Z = 34.76$, $n = 99$, $p = .001$; Figure 2). Second-year females had more curled feathers than first-year females but fewer than adult females (*post hoc* tests; Figure 2). In contrast, we found no differences between males of different ages (Kruskall-Wallis $Z = 3.50$, $n = 87$, $p = .17$; Figure 2). However, the sample for first-year males was small and highly variable, which may have masked effects in this age group. Males in their first and second year had more curled feathers than females of equivalent age (Figure 2). However, there was no detectable sexual dimorphism in curled feather number among adults (Table 1, Figure 2).

The lack of sexual dimorphism in curled feather number is remarkable, given that significant sexual dimorphism exists in other morphological traits (Table 1). Males were 7–10% larger than females in all structural measurements and 26% heavier (Table 1). The curled feather ornament showed more variability than other morphological traits, with a coefficient of variation of 22–24%, compared with 3–10% for other traits (Table 1).

Repeated measurements on the same individuals in consecutive years showed that the number of curled feathers increased by 40–68% between the first and second year in all individuals of both sexes (Figure 3a; Wilcoxon $Z = 2.67$, $n = 9$, $p = .008$). However, there was no clear pattern of increase for males that were measured in both their second and third year (Figure 3a; Wilcoxon $Z = -0.11$, $n = 6$, $p = .92$; no information for third-year females available), suggesting that the number of curled feathers does not increase with age once individuals reach maturity. The differences in numbers of curled feathers between second and third year were <10% for all three individuals (Figure 3a). Furthermore, there was no indication that the number of curled feathers increased in older birds (Figure 3a; Wilcoxon $Z = 1.25$, $n = 31$, $p = .21$). Of 31 adults with changed curled feather number between years,

Table 1
Sexual dimorphism in number of curled feathers and morphological traits in adult black swans (3 years or older)

	Adult males				Adult females				Sexual differences		
Trait	Mean	SE	CV	*n*	Mean	SE	CV	*n*	SDI	*U/t*	*p*
Curled feathers	29.32	0.76	0.22	71	28.16	0.75	0.24	81	0.04	2616	.34
Bill length (cm)	7.03	0.04	0.05	68	6.41	0.03	0.05	83	0.10	11.63	<.0001*
Total head length (cm)	14.16	0.06	0.04	68	13.14	0.04	0.03	83	0.08	13.82	<.0001*
Wing length (cm)	49.64	0.21	0.03	67	45.87	0.45	0.09	75	0.08	7.28	<.0001*
Tarsus length (cm)	9.32	0.09	0.08	69	8.72	0.08	0.09	80	0.07	4.81	<.0001*
Body mass (kg)	6.64	0.07	0.10	85	5.26	0.06	0.10	86	0.26	14.97	<.0001*

Sexual dimorphism index (SDI) is expressed as (mean male trait-mean female trait)/mean female trait). CV = coefficient of variation. Difference in curled feathers compared by Mann-Whitney *U* test. Other variables compared by *t* test.

* Significant differences at a tablewide $p < .05$, using sequential Bonferroni analysis (see Rice, 1989).

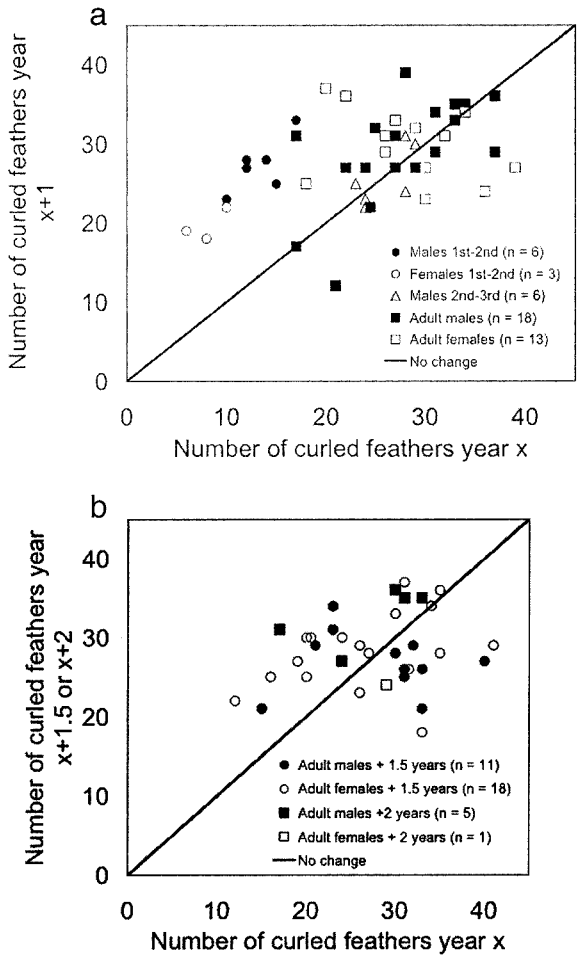

Figure 3
Changes in number of curled feathers in individual birds of both sexes measured in different years and seasons: (a) individuals measured in winters 2000 and 2001, (b) individuals measured in summer 1999 and winter 2000 ($x + 1.5$) or in winter 2000 and winter 2002 ($x + 2$).

16 increased and 11 decreased ($\chi^2_1 = 0.03$, $p = .86$). Adults counted at intervals of 1.5 or 2 years showed more variability (Figure 3b). However, there was no consistent trend with age (Wilcoxon $Z = 0.98$, $n = 35$, $p = .33$); 21 birds showed an increase in curled feather number, whereas 13 showed a decrease ($\chi^2_1 = 1.88$, $p = .17$). Finally, the two oldest individuals in our study population (a ≥10-year-old male and 11-year-old female) did not have unusually large numbers of curled feathers (33 and 16, respectively).

Curled feathers, body size, and condition

In males, the number of curled feathers was positively correlated with body condition (Spearman rank correlation $r_s = .35$, $n = 67$, $p = .009$), but not with tarsus length ($r_s = .08$, $n = 67$, $p = .66$). In females, neither correlation was significant ($r_s = -.09$, $n = 80$, $p = .59$ and $r_s = -.07$, $n = 80$, $p = .57$, respectively). Individual changes in the number of curled feathers between years did not correspond to changes in body mass over the same period for adults of either sex (Spearman rank correlation; males: $r_s = -.04$, $n = 30$, $p = .88$; females: $r_s = -.30$, $n = 30$, $p = .22$).

Curled feathers and social pair formation

Paired male and female swans had significantly more curled feathers than adult (>2 years old) unpaired birds of the same sex (Table 2). Other morphological traits that might affect pairing status (body size, body mass, and body condition) showed no significant differences for either sex after Bonferroni correction (Table 2). The number of curled feathers was also positively correlated between members of a social pair (Figure 4).

Social competition: agonistic interactions, residency status, and reproductive success

Details of 153 interactions between individuals with different numbers of curled feathers were recorded (Table 3). A log-linear model showed that sex, pairing status, and the number of curled feathers all significantly influenced the outcome of agonistic interactions between adults. Males were more likely to win interactions than females (Table 3; $\chi^2_4 = 55.17$, $p = .0001$). Paired birds were more likely to win than unpaired birds (Table 3; $\chi^2_4 = 44.74$, $p = .0001$). The individual with the

Table 2
Comparison between morphological traits of paired and unpaired black swans of both sexes

	Paired individuals				Unpaired individuals				Difference		
Trait	Mean	SE	CV	*n*	Mean	SE	CV	*n*	Ratio	*t*	*p*
Males											
Curled feathers	31.45	0.87	0.19	47	24.81	1.50	0.24	16	1.27	168	.001*
Tarsus length (cm)	9.37	0.11	0.07	44	8.98	0.22	0.10	16	1.04	1.78	.08
Body mass (kg)	6.86	0.10	0.10	47	6.45	0.17	0.10	16	1.06	2.11	.04
Body condition	0.84	0.12	0.92	44	0.50	0.16	1.31	16	1.68	1.56	.10
Females											
Curled feathers	29.93	0.82	0.21	56	24.67	1.39	0.28	24	1.21	369.5	.001*
Tarsus length (cm)	8.65	0.11	0.09	52	8.78	0.15	0.08	24	0.99	0.68	.50
Body mass (kg)	5.26	0.08	0.11	54	5.28	0.09	0.09	24	1.00	0.09	.93
Body condition	−0.60	0.09	−1.03	50	−0.62	0.11	0.89	24	0.97	0.15	.88

CV = coefficient of variation. Difference in curled feathers compared by Mann-Whitney *U* test. Other variables compared by *t* test.
* Significant differences at a tablewide $p < .05$, using sequential Bonferroni analysis (see Rice, 1989).

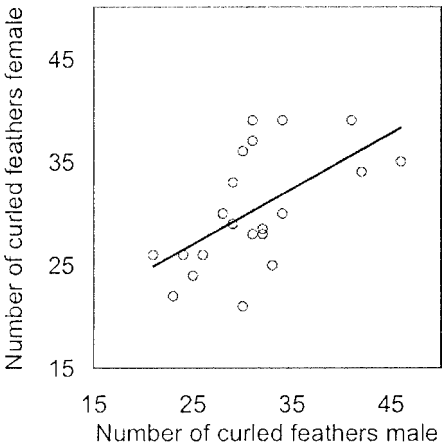

Figure 4
The relationship between the number of curled feathers of males and females of the same pairs (Spearman rank correlation $r_s = .61$, $n = 22$, $p = .003$).

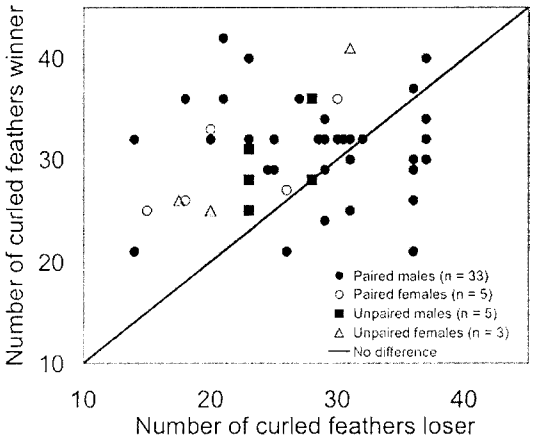

Figure 5
The number of curled feathers on winners and losers of agonistic interactions between same-sex individuals, matched for pairing status (paired or unpaired).

largest number of curled feathers was more likely to win than the individual with fewer curled feathers (Table 3; $\chi^2_4 = 15.32$, $p = .004$). None of the interaction terms was significant (all $p > .30$). Of 40 interactions matched for both sex and pairing status, 28 (70%) were won by the individual with the largest number of curled feathers (Figure 5).

We examined the contribution of paired males and females to agonistic interactions by comparing the frequency of agonistic displays and the time spent in threat display posture during the prebreeding and cygnet-rearing periods. Males were involved in more agonistic interactions and spent more time in threat display posture than females during the prebreeding period (Table 4). During the cygnet-rearing period, only the time spent in threat display posture differed between the sexes (Table 4). The frequency and duration of threat displays did not differ between the prebreeding and cygnet-rearing periods for either sex (Mann-Whitney U tests, all $p > .15$).

Resident pairs had significantly more curled feathers than itinerant pairs but did not differ in body size or mass (Table 5). Large broods are known to enhance the dominance status of breeding pairs in geese (Loonen et al., 1999). However, the average number of curled feathers of the pair remained a significant predictor for residency when brood size was controlled for in a binary logistic model (t ratio = 2.00, $n = 22$, $p = .04$). Addition of tarsus length and body condition reduced the overall significance of the model.

Clutch sizes of resident and itinerant pairs did not differ significantly, but resident pairs had significantly larger broods than itinerant pairs (Table 5). This could be due to differences in hatching success and/or early cygnet mortality. Cygnet survival to 8 months of age was more than twice as high for resident pairs compared to itinerant pairs (Table 5). Although resident pairs had higher numbers of curled feathers and higher cygnet survival, this did not result in a statistically significant correlation between number of curled feathers and cygnet survival (Figure 6). In a generalized linear model, residency status had a near-significant effect on cygnet survival (Δdeviance = 3.30, $n = 20$, $p = .07$), but the number of parental curled feathers did not (Δdeviance = 0.18, $n = 20$, $p = .67$). When only residency status was included, the sample size was larger and the effect highly significant (Δdeviance = 15.94, $n = 64$, $p < .0001$).

Cygnets of resident families spent more time feeding than those of itinerant families (resident: 58.19 ± 2.21 min/1.5h, $n = 26$; itinerant: 45.91 ± 8.16 min/1.5h, $n = 6$). In a backward stepwise general linear model, residency status and time of day significantly affected the cygnets' feeding time ($F_{1,29} = 5.57$, $p = .03$ and $F_{1,29} = 6.10$, $p = .02$, respectively, $n = 32$). Date, brood size, and the interaction between time of day and residency status did not significantly affect the cygnets' feeding time (all $p > .58$). Cygnets of resident pairs also tended to be interrupted less often than those of itinerant pairs (resident: 4.90 ± 2.45, $n = 26$, itinerant: 6.00 ± 1.27, $n = 6$; Mann-Whitney U test $U = 174$, $p = .08$).

Table 3
Outcomes of agonistic interactions between individuals differing in curled feather number

Pairing status (winner–loser)	Sex (winner–loser)	No. of interactions	No. of interactions won by swan with MCF (%)
Paired–paired	Female–female	5	5 (100)
	Female–male	7	3 (43)
	Male–female	21	14 (67)
	Male–male	30	19 (63)
Paired–unpaired	Female–female	5	3 (60)
	Female–male	4	2 (50)
	Male–female	15	11 (73)
	Male–male	26	20 (77)
Unpaired–paired	Female–female	1	1 (100)
	Female–male	3	0 (0)
	Male–female	9	5 (56)
	Male–male	12	4 (33)
Unpaired–unpaired	Female–female	3	2 (67)
	Female–male	2	1 (50)
	Male–female	5	5 (100)
	Male–male	2	2 (100)
Total		153	97 (63)

MCF, most curled feathers.

DISCUSSION

Black swans are sexually dimorphic for most morphological traits, but the curled wing feathers used by both male and female swans in social displays are a genuinely monomorphic

Table 4

Comparison between frequency and duration of agonistic interactions involving pairs during prebreeding (May–July 2000; $n = 35$) and parental care (July–November 1999 and 2000; $n = 48$)

	Agonistic interactions/h						Time in threat display posture (min/h)					
	Males		Females		Difference		Males		Females		Difference	
	Median	QD	Median	QD	Z	p	Median	QD	Median	QD	Z	p
Prebreeding	3	2.0	1	0.5	3.23	.001*	1.73	1.10	0.75	0.56	2.75	.006*
Parental care	2	1.5	2	1.0	1.28	.20	1.43	3.5	0.33	1.63	2.42	.02*

QD = quartile deviation (Zar, 1999). Differences were tested Wilcoxon Signed-Ranks tests.

* Significant differences at a tablewide $p < .05$, using sequential Bonferroni analysis (see Rice, 1989).

ornamental trait, expressed equally in both sexes. The curled feathers also show more variation between individuals than other morphological traits in the black swan, a pattern typical of ornamental traits in birds (Alatalo et al., 1988; Blanco and De la Puente, 2002; Jones and Montgomerie, 1992; Jones et al., 2000). We found that the degree of feather elaboration (measured as the number of curled feathers) correlated with pairing status, social dominance, and, indirectly, reproductive success. Ornamented individuals thus are socially dominant and may be preferred as mating partners.

The full complement of curled feathers is acquired by the second year of age in males, which coincides with the age of first breeding in captive swans (Braithwaite, 1981). Second-year females had fewer curled feathers than adult females and may thus take slightly longer to reach full adult ornamentation. However, ornamentation did not increase with age in adult (3 years and older) birds. Young male barnacle geese *Branta leucopsis* with more adultlike plumage have more trial partners and higher social ranking than those with more juvenile plumage (Van der Jeugd and Blaakmeer 2001). However, we found no indication that second-year black swans that had retained more juvenile plumage characters (black spots in primaries) also had fewer curled feathers.

Social pair formation

Paired individuals of both sexes had significantly more curled feathers than unpaired individuals, suggesting that this ornament may play a role in mutual mate choice. Our finding that the number of curled feathers is correlated between the members of a social pair further strengthens this view. Little is known about courtship and the process of pair formation in this species. In geese, the triumph ceremony is known to play an important role in pair formation (Bigot et al., 1995; Choudhury and Black, 1993), and there is anecdotal evidence that the same is true for the black swan (Kraaijeveld and Mulder, 2002). The curled feathers feature prominently in social displays such as the triumph ceremony in this species and could conceivably be used in mate assessment. Pairing in the closely related mute swan *C. olor* is known to be assortative with respect to age (Perrins and McCleery, 1997), and this may also be true for the black swan. However, there was no evidence for a strong effect of age on the number of curled feathers. Thus, age-assortative mating is unlikely to explain the correlation between pairing and ornamentation. Nevertheless, other factors such as similar environmental conditions experienced by members of a pair (e.g., food availability) may lead to similar ornamentation and require experimental evaluation.

The direction of sexual selection depends on the relative roles of the sexes in parental care (Kokko and Monaghan, 2001; Parker and Simmons, 1996; Trivers, 1972). Generally, the sex providing less care should be more active in competition over mates (Trivers, 1972). In the black swan, males are more active in competition over feeding areas, which is an important part of the parental effort. Males also provide most of the incubation effort (Brugger and Taborsky, 1994). Competition among females over high-quality males might thus be

Table 5

Comparison between reproductive success and morphology (mid-pair values) of resident and itinerant pairs (see text for definitions)

	Resident pairs				Itinerant pairs				Difference		
Parameter	Mean	SE	CV	n	Mean	SE	CV	n	Ratio	U/t	p
Reproductive success											
Clutch size	5.03	0.18	0.20	31	4.40	0.21	0.24	25	1.14	267.5	.04
Brood size	4.29	0.23	0.33	38	3.22	0.27	0.44	27	1.33	309.5	.006*
Number of surviving cygnets	2.13	0.23	0.67	38	0.78	0.19	1.25	27	2.73	231	<.0001*
Cygnet survival	0.51	0.05	0.66	38	0.22	0.06	1.34	27	2.32	263	.001*
Morphology											
Curled feathers	33.42	1.33	0.14	13	27.28	1.25	0.14	9	1.22	19	.008*
Tarsus length (cm)	8.95	0.20	0.08	13	9.31	0.24	0.08	10	0.96	1.17	.26
Body mass (kg)	6.06	0.12	0.08	17	5.85	0.13	0.08	14	1.04	1.19	.24
Body condition	0.11	0.13	4.40	12	0.03	0.17	17.08	10	3.67	0.36	.73

Difference in tarsus length and body mass were compared by t test. All other variables were compared by Mann-Whitney U tests.

* Significant differences at a tablewide $p < .05$, using sequential Bonferroni analysis (see Rice, 1989).

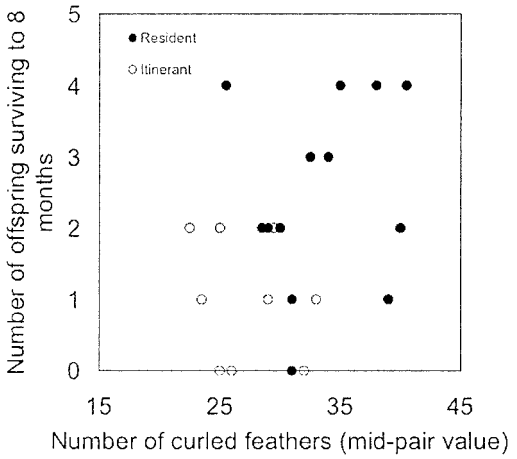

Figure 6
The relationship between the average number of curled feathers of the pair and number of surviving cygnets (Spearman rank correlation $r_s = .32$, $n = 22$, $p = .31$). Residency status of pairs is indicated (see text for definitions).

more intense than competition among males over females, as has been described in another mutually ornamented species, the moorhen *Gallinula chloropus* (Petrie, 1983).

Barnacle geese compare up to six potential partners before a stable pair bond is formed (Choudhury and Black, 1993; Van der Jeugd and Blaakmeer, 2001), and a similar system may operate in the black swan. Although individuals may continue comparing potential partners even after pair formation has taken place (Black, 1996), low divorce rate (6% in our study population; Kraaijeveld, unpublished data) and high survival should limit the number of realized opportunities for mate choice. It therefore appears likely that social factors in addition to sexual competition also select for mutual ornamentation in the black swan.

Social dominance

The ornamental feathers are most conspicuously displayed during agonistic displays and during the triumph ceremony. Both function as threat signals toward conspecifics (Kraaijeveld and Mulder, 2002). Our finding that individuals with many curled feathers are dominant over same-sex individuals with fewer curled feathers in agonistic interactions suggests that the curled feathers play a role in social competition over resources. In addition to potential mates, such resources may include food and nesting space. In our swan population, prolonged access to suitable feeding habitat for the cygnets ("residency") is clearly an important resource that directly affects the survival prospects of cygnets.

Resident pairs had significantly more curled feathers than itinerant pairs, probably because curled feathers signal competitive ability and thus improve an individual's chances of gaining access to preferred areas and maintaining tenancy of these areas for a prolonged period. Competitive ability may depend on several factors, including body size, body condition, age, breeding experience, and motivation. We found a correlation between the number of curled feathers and body condition in males, suggesting possible condition dependence of the ornament. Correlations between body condition and the expression of a mutual ornament have been reported in one or both sexes for a number of species (magpie *Pica pica*: Blanco and De la Puente, 2002; inca tern *Larosterna inca*: Velando et al., 2001; crested auklet: Jones et al., 2000). However, we failed to obtain the same result when repeated measurements of the same individual were considered, and we therefore interpret this result cautiously.

Males are more active than females in social competition over resources other than mates. The role of social competition over nonsexual resources in the maintenance of the curled feather ornament may therefore be stronger in males than in females. As with the potential sex bias in sexual selection, this suggestion parallels findings in the moorhen, in which males compete over territories (Petrie, 1984). Both sexes in the moorhen use the red frontal shield as an indication of dominance (Petrie, 1984, 1988). In crested auklets, males are also the more aggressive sex, whereas females may be more active in defending mates (Jones and Hunter, 1999). Given these apparently different balances of selective forces between males and females, it is puzzling why ornament expression remains the same in males and females of black swans, moorhens, and crested auklets.

Status signaling may be particularly advantageous in high population densities, where individuals frequently encounter unfamiliar individuals (Rohwer, 1975; Whitfield, 1987). It is interesting to note in this respect that the black swan is both the only species in its genus with a feather ornament and also the only species that regularly breeds in colonies (Scott and the Wildfowl Trust, 1972). However, several other swan species have elaborate bill ornaments (e.g., black-necked swan *C. melanocoryphus*; mute swan) and threat displays that involve lifting of the wings (mute swan; Johnsgard, 1965), and the absence of feather ornaments in these species might reflect a lack of selectable variation.

Reproductive success

For social competition to lead to selection, it must have an effect on the fitness of competing individuals (Tanaka, 1996). Cygnet survival of pairs that are able to maintain residency in a patch of habitat on the lake foreshore was more than twice as high as that of itinerant pairs. One likely factor contributing to this improved survival is our finding that cygnets of resident pairs spent more time feeding than those of itinerant pairs. Similar benefits accrue to juvenile barnacle geese and bewick's swans *C. bewicki* with dominant parents (Black and Owen, 1989; Scott, 1980). Aggressive parents may also be able to provide better protection against predators. Nevertheless, the causality may also be reversed; in barnacle geese, larger families are more dominant (Loonen et al., 1999), and high cygnet survival may help parents to maintain residency. In black swans, however, the number of curled feathers was a better predictor of residency than was brood size.

Honesty of the signal

The prominence of the ornament in agonistic displays, the correlation between within-sex social dominance and ornamentation, and the association between ornamentation and residency status all suggest that the display feathers function as a badge of status. Such signals allow dominant individuals access to resources, while minimizing their aggressive interactions with subordinate individuals (Dawkins and Krebs, 1978; Rohwer, 1975; Rohwer and Rohwer, 1978). For such a signaling system to be evolutionarily stable and prevent poor-quality individuals from cheating, it must be costly (Pomiankowski et al., 1991; Zahavi and Zahavi, 1997). The physiological or energetic costs of growing and maintaining the display feathers (extra resources allocated to make the feather curled, aerodynamic costs, etc.) are likely to be trivial. However, the ornament could carry a substantial social cost if dominant individuals frequently test the signaling system (Johnstone and Norris, 1993; Møller, 1987; Whitfield, 1987).

Two recent studies found evidence for such dominance testing (Molles and Vehrencamp, 2001; Parker and Ligon, 2002), but the generality of these findings remains to be established. Alternatively, high levels of ornament expression may depend high levels of circulating testosterone, which may incur secondary costs such as high metabolic rate (Buchanan et al., 2001), high ectoparasite load (Poiani et al., 2000), and low immunocompetence (Evans et al., 2000).

Interactions between selective forces

Mate choice, competition over mates, and competition over other resources are not mutually exclusive processes, and their effects are likely to be additive (West-Eberhard, 1983). In species with biparental care, an individual's own attractiveness as a mate is expected to affect its access to potential mates, which should result in assortative pairing (the differential access hypothesis; Burley, 1986). It seems likely that as biparental care evolved from female-only care, males displayed increasing selectivity of mates (Burley and Johnson, 2002). In the black swan, cooperative parental defense of cygnet feeding areas has a positive effect on offspring survival and therefore on fitness of both members of the pair. Breeding adults thus gain fitness benefits from pairing with a socially dominant partner, and this may explain why ornament-assortative pairing occurs in the black swan. In crested auklets, individuals with longer crests are dominant over individuals with shorter crests and are also preferred as mates (Jones and Hunter, 1999). Nonsexual competition (e.g., over nesting sites and chick defense), is also likely to be important in crested auklets (Fraser et al., 2002; Jones and Hunter, 1999). Nevertheless, the relative importance of sexual versus nonsexual competition in maintaining a mutual ornament may differ across species.

Our study demonstrates reproductive benefits related to the expression of a mutual ornament. The proximate mechanism through which this benefit is achieved is the signaling of social dominance. Individuals benefit from pairing with a socially dominant partner, and the curled feathers therefore play a role in mate choice. The evolution and maintenance of the ornament is therefore not simply the consequence of sexual selection but should be considered in the broader context of social selection.

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